

Six New Taxa of *Passiflora* (Passifloraceae), with Nomenclatural Notes on the Genus in Mesoamerica

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ABSTRACT. Nomenclatural notes, lectotypifications, a neotypification, and changes in synonymy affecting *Passiflora* (Passifloraceae) in Mesoamerica are presented, as well as descriptions of new varieties and species. Included are six new taxa: *P. cissampeloides*, *P. ornithoura* var. *chiapasensis*, *P. quetzal*, *P. quinquangularis*, *P. subfertilis*, and *P. veraguasensis*. Two taxa change rank: *P. sublanceolata* is elevated from *P. palmeri* var. *sublanceolata* Killip and *P. jorullensis* var. *salvadorensis* is lowered from *P. salvadorensis* J. D. Smith. The new combination *P. platyloba* var. *pubescens* (Grisebach) J. MacDougal must be substituted for *P. platyloba* var. *williamsii* (Killip) A. Gentry, and *P. serrulata* var. *pubescens* Grisebach is a synonym of *P. williamsii* Killip, not *P. vitifolia* HBK. The well-known name *P. pulchella* HBK is a new synonym of *P. bicornis* Miller; *P. brevipes* Killip is a new synonym of *P. cobanensis* Killip; *P. guatemalensis* S. Watson is not a synonym of *P. hahnii* (Fournier) Masters; *P. cookii* Killip is a new synonym of *P. hahnii*; and *P. obscura* Lindley is a new synonym of *P. sexflora* Jussieu. Lectotypes are designated for *P. divaricata* Grisebach (*Duchassaing s.n.*, anno 1850, GOET), *P. serrulata* β. *pubescens* Grisebach (*Duchassaing s.n.* [1850–1851], GOET). The colored plate opposite page 430 in *Revue Horticole* 40 (1869) is designated as the neotype of *P. hahnii*.

Key words: Mesoamerica, *Passiflora*, Passifloraceae, S. Calderón.

Approximately 20% of the genus *Passiflora* L. grows in Mesoamerica, that area from southeastern Mexico through Panama. These 106 species are predominately members of the small-flowered and small-fruited passionflowers, subgenus *Decaloba* (DC.) Reichenbach. The last monograph of *Passiflora* (Killip, 1938) recognized about 70 species of the genus in Mesoamerica, and I and others have added numerous others in the last 20 years (e.g., Knapp & Mallet, 1984; MacDougal & Hansen, 2003). The genus has traditionally been divided into at least 22 subgenera (Killip, 1938). Here I use the recently published infrageneric classifica-

tion by Feuillet and MacDougal (2003) that recognizes only four subgenera. The following new taxa and nomenclatural notes are the result of the preparation of a treatment of the Passifloraceae, still in press, for the *Flora Mesoamericana* project, and are published here in advance in order to make the new and correct names generally available. In the treatment of notes and novae below, accepted names are listed alphabetically.

Passiflora bicornis Houston ex Miller, Gard. Dict. ed. 8, Passiflora no. 13, 1768 [as “*Bicornia*”]. TYPE: Colombia. [Bolívar: near Cartagena], *Houston s.n.* (holotype, BM, photo at BH, NY, US).

Passiflora pulchella HBK, Nov. Gen. Sp. 2: 134. 1817. Syn. nov. TYPE: Venezuela. Aragua: Cura, “prope Cura (Valles de Aragua & Orinoco),” *Humboldt & Bonpland 1134* (lectotype, selected by Killip (1938: 226), B destroyed, photo at F neg. 16554, MO; isotype, B-W not seen, P).

Passiflora divaricata Grisebach, Bonplandia 6(1): 7. 1858. TYPE: Panama. Anno 1850, *Duchassaing s.n.* (lectotype, designated here, GOET).

Miller’s older name supplants the widely known *Passiflora pulchella* of floras from Mexico to Venezuela. Killip (1938: 226) suspected this: “This may well be . . . *Passiflora bicornis* . . . but Miller’s description is indefinite . . . in the absence of a type specimen, it seems best to maintain the name that is in general use.” Examination of the type found at BM, with its well-preserved flower, large bracts, and bilobed leaves, now shows *Passiflora bicornis* to be an older name for the same species.

Killip (1938) also suggested that the type of the synonym *Passiflora divaricata* was a Duchassaing specimen at P, but in Grisebach’s herbarium at GOET there are three elements from Duchassaing that appear to have been part of Grisebach’s protologue. One is a watercolor painting with violet flowers, one has a divaricate branch described in the protologue, and one is marked in Grisebach’s hand “[*Passiflora*] *divaricata* m.” I have chosen the last element as lectotype.

As a synonym of *Passiflora pulchella*, Killip

(1938) cited the ineffectively published name *Passiflora subtriangularis* [no rank] *beta* S. Calderón, Datos Bot. Médica El Salvador (Passifloras Dilibatas de El Salvador) 11, figures 9, 10, plate opp. p. 12. pre-1936. For a discussion of the validity and availability of Calderón's publication, see below under *P. quinquangularis* S. Calderón ex J. MacDougal.

***Passiflora cissampeloides* J. MacDougal, sp. nov.**

TYPE: Honduras. Cortés: trail to Cerro Cantilles, Cusuco National Park, 15°30'N, 88°14'W, 1840 m, 18 Mar. 1993 (fr), *T. Hawkins* 634 (holotype, EAP; isotypes, HEH not seen, MO, TEFH not seen). Figure 1.

Haec species *Passiflorae guatemalensis* similis, sed ab ea stipulis glandularibus integris vel leviter crenatis, bracteis minoribus, fructu ellipsoideo manifeste stipitato atque seminibus insigniter minoribus distinguitur.

Vine, to 10 m, glabrous throughout; stems terete, glaucous; prophylls of the vegetative bud 2, unequal, 0.9–2.2 × 0.4–0.8 mm, both narrowly ovate, acuminate, entire or rarely with a marginal tooth. Stipules 4–8 × 11–16 mm, depressed-ovate, auriculate, slightly clasping, truncate at apiculate apex, the margin entire to obscurely crenulate and 3- to 6-glandular; petioles eglandular; blades 5–6.5 × 5–6.7 cm, peltate 8–10 mm from margin, entire, not variegated at maturity, widely ovate, at base subtruncate with convex curve in peltate region, obscurely 3-lobed, angle between lateral veins 50°–60°, the lateral lobes ± obsolete, the central lobe acute or bluntly acute; laminar nectaries absent or marginal when present, as 1 or 2 glands borne at edge of peltate region. Peduncles 1 per node, (1.4–)2.0–3.2 cm, uniflorous; bracts 2 at apex of peduncle, variable in size, 6–15 × 9–17 mm, ovate-triangular, free to base, entire or with a very few minute setae proximally, not glandular, acute at apex, green. Flowers “creme color, centre yellow” (*Hawkins* 198), the corona apparently yellow; stipe ca. 3 mm long (to 4.5 mm in fruit); hypanthium 17–18 mm diam.; sepals 11–15 × 12–17 mm, widely oblong triangular, rounded at apex, with no projection; petals 16–17 × 12–13 mm, widely ovate, abruptly narrowed at base; coronal filaments in 3 to 4 series, the outermost 5–8 mm long, linear, the inner 2 to 3 series 3–5 mm long, capitellate; operculum membranous, plicate; androgynophore 8–9 mm, anthers ca. 6 mm; ovary 3–4 × 2–2.5 mm, ellipsoid, glabrous; styles 5 mm long including stigmas. Fruit ca. 8 × 3.5–4 cm including a 1.5–2.0 cm long stipe, ellipsoid, lustrous; seeds 4.5–4.9 × 2.7–2.8 × 1.3–1.5 mm thick, narrowly obovate in outline,

campylotropous, the testa reticulate with ca. 60 pits, the chalazal beak inclined toward the raphe.

With a peltate leaf similar to *Passiflora guatemalensis* S. Watson or some lowland forms of *P. hahnii* (Fournier) Masters, and a stipitate fruit like *P. membranacea* Benthham, this new species combines character states from each of the other species in supersection *Hahniopathanthus* (Harms) J. MacDougal & Feuillet, to which this species clearly belongs. From *P. membranacea*, which has leaves peltate only 1–3.5(–5) mm from the margin, peduncles (6.3–)8–14(–17.5) cm long, bracts 2.7–5.0 × 2.5–5(–6.3) cm, and androgynophore (2.7–)3.0–4.0 cm long, it is easily distinguished by the peltate leaf, shorter peduncles, smaller bracts, and much smaller flower. From *P. guatemalensis*, which has dentate-fimbriate stipules with filiform teeth, androgynophore 3.5–5.0(–6.0) mm long, and a non-stipitate fruit or the stipe 1 mm long or less, it differs by the entire or crenate stipules with glandular margins, the longer androgynophore, and the stipitate fruit. It differs from *P. hahnii*, which has bracts 1.9–6.2 × 1.5 × 6.4 cm, peduncles 2.5–7.0 cm, and a fruit stipe of 1–4 mm, in the smaller bracts, usually shorter peduncles, and the stipitate fruit. *Passiflora cissampeloides* has generally smaller bracts than the others in the supersection, and the seeds are markedly smaller than the other known species, which range from (4.6–)5–6.5 × (3.1–)3.3–4.2(–4.5) mm.

Distribution and habitat. Known from Copán and Cortés, Honduras, at 1460–1840 m. The type was collected in moist cloud forest of pine, *Liquidambar*, *Podocarpus*, and *Quercus*. The paratype is from dense mixed hardwood forest.

Etymology. The peltate leaves of this new species very much resemble species of *Cissampelos* L. in the Menispermaceae, hence the specific epithet.

Paratype. HONDURAS. **Copán:** S slope of Cerro Azul directly N and above Quebrada Grande, 12 km NE of Florida, Cerro Azul National Park, 15°06'N, 88°55'W, 9 Feb. 1992, *T. Hawkins* 198 (EAP, MO).

***Passiflora cobanensis* Killip, J. Wash. Acad. Sci. 14: 111. 1924. TYPE:** Guatemala. Alta Verapaz: between Chamá and Cobán, 3000 ft. [“950 m” in protologue], 26 July 1920, *H. Johnson* 411 (holotype, US-1083984, photo at F).

Passiflora brevipes Killip, Publ. Carnegie Inst. Wash. 461: 312, plate 2. 1936. Syn. nov. TYPE: Belize. Toledo: Jacinto Hills [ca. 16°09'N, 88°55'W], 400 ft. [“120 m” in protologue], 11 Mar. 1934, *W. A. Schipp* 1304 (holotype, F-733685, neg. 52921; isotypes, A not

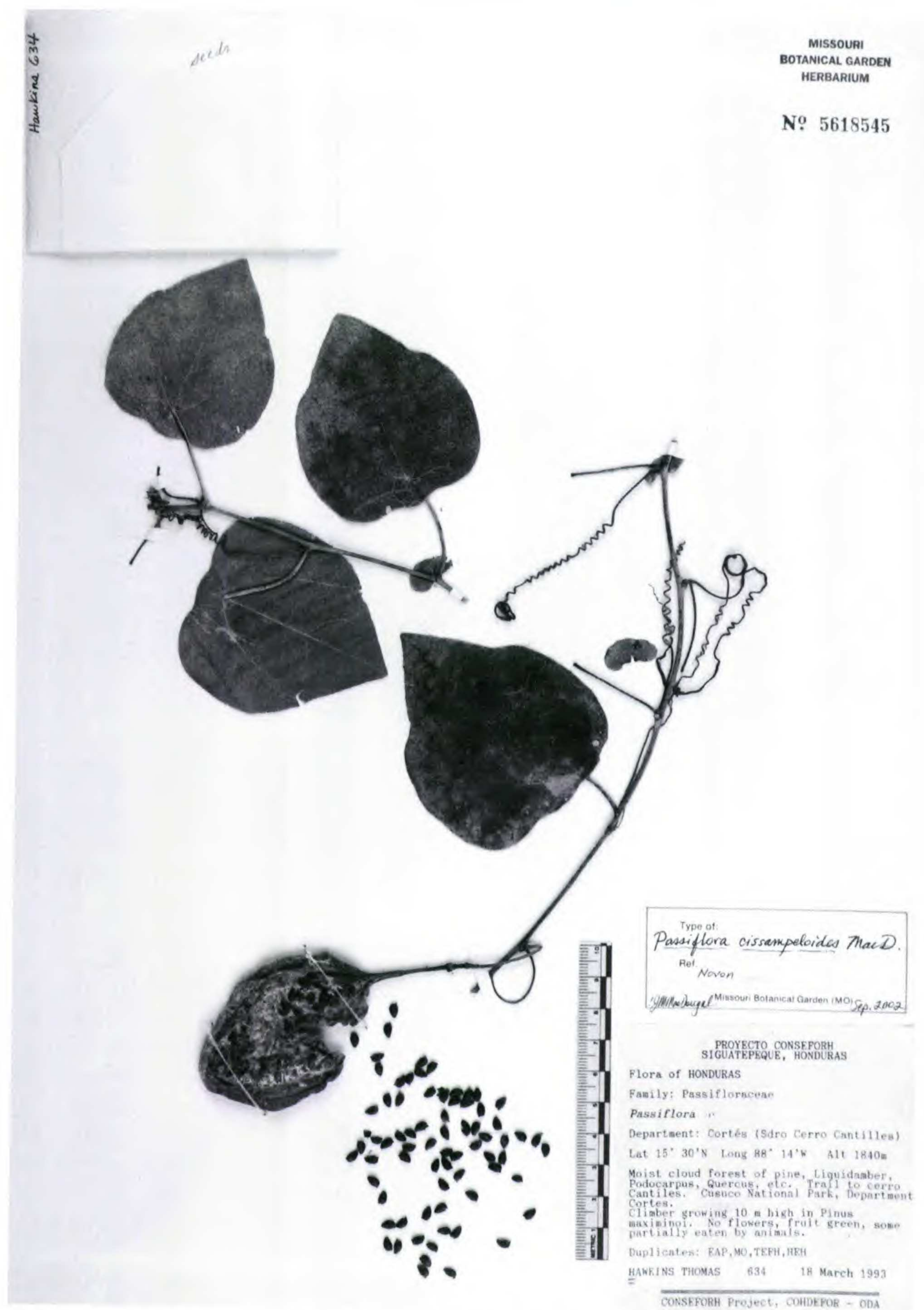


Figure 1. Photograph of the isotype of *Passiflora cissampeloides* at MO.

seen, G not seen, GH not seen, MICH photo at DUKE, MO, NY).

Even at the time of his 1938 monograph, Killip knew both of these passifloras only from their type collections. They are unusual in that they have un-

lobed leaves in section *Xerogona* (Rafinesque) Killip, a group with otherwise strictly bilobed leaves, and share this leaf shape as a uniquely derived character. The type specimens of the two names represent the extremes in leaf morphology of what

I now take to be single species, *Passiflora cobanensis*. The combined range is the Atlantic lowland humid forest to lower montane rainforest, especially on ridges and limestone outcrops, of Chiapas, Mexico, through central Guatemala to Belize, at elevations of 120–1700 m. The type of *P. cobanensis* represents a mesic to wet upland form, not uncommon in parts of Chiapas, Mexico, with longer, narrower, thinner leaves and less pubescence. The more recent name synonymized here, *P. brevipes*, represents a lowland form from hotter and seasonally drier areas with proportionately wider and thicker leaves and denser pubescence. There does not appear to be a definite geographical disjunction. During the revision of this group for *Flora Mesoamericana*, I have seen a number of well-prepared flowering and fruiting sheets of this species representing both forms and intermediates between them. I have grown and flowered the squat lowland form from Belize. The stem on the lowland form tends more toward triangular, and the floral stipe is often shorter than in the upland form, but I find no basis to Killip's suggestion that the flowers differ significantly, and the fruits and seeds are certainly the same. This is a case of ecological and regional differentiation, but not at a level that deserves species status.

Passiflora hahnii (Fournier) Masters, Trans. Linn. Soc. London 27: 638. 1871. *Disemma hahnii* Fournier, Rev. Hortic. 40: 430, pl. opposite. 1869. TYPE: the cited plate, neotype here designated.

Passiflora cookii Killip, J. Wash. Acad. Sci. 12: 256. 1922. Syn. nov. TYPE: Guatemala. Alta Verapaz: near Finca Sepacuité, 13 Apr. 1902, O. F. Cook & R. F. Griggs 593 (holotype, US 408302, photo at F).

The protologue of *Disemma hahnii* consists of a diagnosis by Fournier, a discussion and further description of living material by B. Houlet, and a fine color plate. The discussion indicates that the species was sent by Hahn from Mexico in 1857 and grown at the Jardin des Plantes, Muséum National d'Histoire Naturelle, in Paris. I have not been able to locate a type specimen. A suitable type would be a garden-derived element at P labeled in Fournier's or Houlet's hand, rather than one of Ludwig Hahn's widely distributed Mexican collections, most of which were collected later, in 1865–1866. Nevertheless, Killip (1938: 233) cited "Mexico: Hahn (K, type collection)"; whether he meant this as a lectotypification or was just following Masters's citations (1871, 1872) is not clear.

In all of his publications, Killip had a mistaken

impression of the identity of *Passiflora hahnii*. He obviously never saw the gorgeous and informative colored plate in the protologue of the basionym, which so clearly shows the diagnostic stipules, leaf blades, bracts, and flowers. The true *P. hahnii* has entire (or crenate) stipules, most unlike Killip's key character of "stipules setiferous-toothed" (1938: 49), which is diagnostic instead for the closely related *P. guatemalensis*, a name overlooked by Killip entirely. The circumscription of Killip's *P. cookii* falls within the morphology described for *P. hahnii*. On the other hand, in revising this group for *Flora Mesoamericana*, I have found much variation in *P. hahnii*, including great variation in bract size and number of coronal series. There is some degree of correlation with elevation; e.g., forms represented by the type of *P. cookii*, with a low coronal number and subtruncate laminar base with reduced laminar nectaries, seem to be a lowland variation. I have been unable to separate any taxa from this complex, however, so now treat *P. cookii* as a synonym of *P. hahnii*. This species complex deserves further study.

Passiflora jorullensis HBK var. ***salvadorensis*** (J. D. Smith) J. MacDougal, comb. et stat. nov. Basionym: *Passiflora salvadorensis* J. D. Smith, Bot. Gaz. (Crawfordsville) 42: 297. 1906. TYPE: El Salvador. San Salvador: San Salvador, May 1905, L. V. Velasco & J. D. Smith 8887 (holotype, US 941598; isotypes, GH, US).

Passiflora salvadorensis had been maintained as a distinct species by Killip (1938), who distinguished it from *P. jorullensis* HBK on the basis of its pink rather than orange flower, its leaves lobed to below the middle rather than $\frac{1}{3}$ their length, and its stems and petioles glabrous rather than puberulent. Additionally, one was supposed to inhabit Mexico, the other El Salvador. We now know from additional collections that the two are so closely related that the flowers are nearly identical and they overlap on many other morphological characters. Except by geography, I am unable to consistently distinguish them. They do usually inhabit different forest types, however, and some morphological differences are correlated with geographical range (see key below), so it seems preferable to distinguish them here as varieties.

KEY TO THE VARIETIES OF *PASSIFLORA JORULLENSIS* IN MEXICO AND CENTRAL AMERICA

- 1a. Internodes of stems lightly puberulent to pubescent; leaves 2(to sub 3)-lobed ca. $\frac{1}{4}$ – $\frac{1}{3}$ (rarely to ca. $\frac{1}{2}$) the distance to the base, the lobes acute

- to obtuse, rarely somewhat rounded; plants of 1000–1700 m elevation, Nayarit to Guerrero, Mexico var. *zorullensis*
- 1b. Internodes of stems glabrescent; leaves 2-lobed ½ the distance to the base or slightly deeper (rarely only ⅓–½), the lobes obtuse to broadly rounded, rarely subacute; plants of 150–1000 (rarely to 1600 in Chiapas) m, SE Oaxaca, W Chiapas, Mexico, and El Salvador var. *salvadorensis*

There is no basis for separation of these taxa by the nearly identical flowers. Both are the same size, with strictly one row of coronal filaments, a 3–4 mm long suberect operculum that is sparsely puberulent basally, and a 9–11 mm long androgynophore. The flowers of both exhibit the same unusual behavior of remaining open more than one day (pers. obs.; Calderón, s.d.). In both, the corona is initially red or a fiery red-orange, which persists for the first day, but changes or fades the second day to purple or purple-pink before closing later that evening or even the morning of the third day. The odor of *Passiflora zorullensis* var. *salvadorensis* is unknown, but the typical variety is famously stinky with a strong odor described as between “stercoraire et putride” by Planchon (1849). A two-day flower is unique among the native species of passifloras in Mesoamerica, and is shared in Mexico and North America only by the red variant of the close relative *P. mexicana* Jussieu. The pollination system associated with this unusual floral behavior is not known. Dennis Breedlove has seen hummingbirds at the flowers of variety *salvadorensis* in Cintalapa, Chiapas, at 1600 m (pers. comm.), wasps have been seen at the flowers of the red *P. mexicana*, and both wasps and hummingbirds at the flower of the related (and also malodorous) *P. gilbertiana* J. MacDougal.

As noted by Killip (1938), the leaf shape is often distinctive, with the leaves of *Passiflora zorullensis* var. *salvadorensis* more deeply lobed and the lobes generally obtuse or rounded, but there is overlap between the varieties. Both occasionally retain some costal variegation into maturity. The leaves of variety *salvadorensis* closely resemble several *Bauhinia* species with which the variety often grows. The differences in vestiture are generally ones of quantity rather than quality: although variety *salvadorensis* often appears glabrous at first glance, close examination reveals a slight puberulence at least on the young growth or around the nodes. The type and other material from El Salvador is particularly glabrescent, with ovaries that are glabrous or very nearly so. In variety *zorullensis*, glabrous ovaries are seen only in the westernmost populations in Mexico.

These two disjunct taxa are usually found in ecologically different forest types. *Passiflora zorullensis* var. *zorullensis* mainly inhabits moist montane oak forest, while variety *salvadorensis* is usually found in subdeciduous or tropical deciduous forest, yet sometimes ranges up to montane moist forest. Neither variety of the species is known from Guatemala or Honduras.

As a synonym of *Passiflora salvadorensis*, Killip (1938) cited the ineffectively published name, *Passiflora subtriangularis* (no rank) *alfa* S. Calderón, Datos Bot. Médica El Salvador (Passifloras Dilo-batas de El Salvador) 15, figures 11, 12, plate opp. p. 20, pre-1936. That name is accompanied by a detailed protologue with valuable morphological and ecological information about this variety. For a discussion of the validity and availability of Calderón’s publication, see below under *P. quinqueangularis* S. Calderón ex J. MacDougal.

Representative specimens examined. EL SALVADOR. **Ahuachapán:** San Benito, al S del pie del cafetal El Naranjo, Co. Davila, E. Sandoval & Chinchilla 574 (MO). **San Salvador:** San Salvador, S. Calderón 810 (US); camino al cerro de San Jacinto, 21 July 1959, E. Montalvo 3662 (ENCB); vicinity of San Salvador, P. Standley & Padilla 2951 (EAP). MEXICO. **Chiapas:** Mex. Hwy. 190, 13 mi. SE of Tapanatepec, 11 Sep. 1964, D. Breedlove 7167 (DS, ENCB, F, LL); Arriaga, 13 km N of Arriaga along Mex. Hwy. 195, 25 Sep. 1971, D. Breedlove 19848 (DS, ENCB, MICH); Cintalapa, SE of Cerro Baul on the border with the state of Oaxaca, 16 km NW of Rizo de Oro along logging road to Colonia Figaroa, 6 Sep. 1972, D. Breedlove 27627 (DS); Cintalapa, along Rt. 190, 14.7 mi. E of intersection of Rt. 200 to Tapachula, 8 Aug. 1978, vicinity of Tonalá, 18 Aug. 1949, E. Matuda 18783 (F, MEXU); Tuxtla Gutierrez–Jalisco, Sep. 1923, Purpus 9257 (DS). **Oaxaca:** San Pedro Tapanatepec, along Rt. 190, 5.9 mi. E of intersection of Rt. 200 to Tapachula, 8 Aug. 1978, J. MacDougal 326 (DUKE).

Passiflora ornithoura Masters var. **chiapasensis** J. MacDougal, var. nov. TYPE: Mexico. Chiapas: Mt. Ovando [15°25’N, 92°36’W], 2000 m, 14–18 Nov. 1939, E. Matuda 3971 (holotype, MEXU; isotypes, GH, MICH—2 sheets, MO, US). Figure 2.

Haec varietas a varietate typica floribus seminibusque majoribus, foliorum plerumque minus profunde lobatorum lobis lateralibus angulum minorem inter se formantibus atque filamentis coronalibus in seriem unicam dispositis distinguitur.

Herbaceous vine, size unknown but probably 2–5 m, minutely puberulent throughout at the shoot tip (except blades), becoming sparsely puberulent (to glabrescent) below. Stems ± terete, striate, puberulent or sparsely puberulent (rarely glabrescent) below; prophyll of vegetative bud 1, narrowly lan-



Figure 2. Photograph of the holotype of *Passiflora ornithoura* var. *chiapasensis* at MEXU.

ceolate (rarely 3-toothed). Stipules 2–4(–5.5) × 0.2–0.5 mm, linear-triangular or narrowly triangular, subfalcate, usually proximally purple and apically stramineous to necrescent; petioles eglandular; blades (2–)3.5–12(–15) cm long in outline,

(1.5–)2.5–5(–8) cm along central vein, (2–)3–8(–9) cm wide, entire, almost glabrous or often very sparsely puberulent basally or on the basal primary veins, sometimes variegated along the lateral veins at maturity, truncate-obovate to very widely obovate

or shallowly obdeltate, 2-lobed 0.08–0.38(–0.58) the distance to the base, or ca. 3-lobed less than 0.2 the distance to the base, the lateral lobes broadly lanceolate to shallowly triangular, acute to obtuse (rounded), the central lobe (obsolete or truncate) obtuse, the central vein always shortest; the angle between the lateral veins (21°–)26°–46°(–62°), the ratio of laminar width to (central lobe) length (0.64–)0.75–1.5(–2.6); laminar nectaries borne between the main veins, often 4 or less on smaller leaves, rarely absent on some leaves of a branch. Peduncles 2 per node, 0.9–2.5 cm, uniflorous; bracts (1–)1.5–4 × 0.2–0.6 mm, linear-triangular to narrowly lanceolate, distally necrescent. Flowers light green to pale green-yellow, the corona reddish or orange basally, orange to yellow apically; hypanthium 5–7 mm diam.; stipe 2.5–5 mm; sepals 9–11.5 × 3–4.3 mm, lanceolate-oblong, with no projection, light green or light green-yellow; petals 4–6 × 1.5–2 mm, narrowly ovate-oblong, pale green; coronal filaments in 1 series, 1.8–3 mm long (or in Guatemala, rarely with a trace of a second inner row), clavate; operculum ca. 1.5 mm long, membranous, plicate, light yellow with tinge of pink; staminal filaments connate 3.5–4.5(–5.0) mm along the purple-pink androgynophore, the free portions 5–6 mm; anthers 2.5–2.7 mm long; ovary 1.2–2.1 × 1.1–1.9 mm, subglobose, glabrous, the styles 6–7.5 mm long including stigmas. Fruit 0.9–1.5 cm diam., globose (to slightly obovate), purple-black, estipitate; arils unknown; seeds 3.1–3.6 × 2.1–2.6 × 1.5 mm, obovoid, transversely sulcate with (6)7 to 9 sulci, the intervening ridges verrucose; seeds per fruit 4 to 25.

KEY TO THE VARIETIES OF *PASSIFLORA ORNITHOURA* IN MEXICO AND CENTRAL AMERICA

- 1a. Leaves 2-lobed 0.08–0.38(–0.58) the distance to the base, or 3-lobed less than 0.2 the distance to the base, the angle between the lateral veins 21°–46°(–62°), the ratio of laminar width to central vein length 0.64–1.5(–2.6); floral stipe 3.3–5 mm; sepals 9–11.5 mm; coronal filaments 1-seriate (or rarely with a trace of second, inner row) var. *chiapasensis*
- 1b. Leaves 2-lobed (0.48–)0.65–0.90 the distance to the base, the angle between the lateral veins 35°–75°(–81°), the ratio of laminar width to central vein length 2.4–10(–15); floral stipe 1.4–3.5 mm; sepals 6–8.5 mm; coronal filaments 2-seriate (the inner row often reduced and inconspicuous) var. *ornithoura*

Passiflora ornithoura var. *chiapasensis* differs from the typical variety of *P. ornithoura* Masters primarily in having larger flowers and seeds, the coronal filaments in only one series, and leaves that are usually less deeply lobed, with a smaller angle

between the lateral lobes. There is only slight overlap in leaf shape with the typical variety, and thus the varieties can usually be identified in the absence of flowers or seeds (see key above). The laminar nectaries often number five or less per leaf, and can be reduced to the point of absence on some but not all leaves of a particular flowering branch (e.g., Téllez & Pankhurst 6983). Reduction in laminar nectaries is also sometimes found in forms of the typical variety (e.g., the type specimen, *J. Donnell-Smith* 2143, of the synonym *P. dictiophylla* Masters). Leaves of some collections of *P. ornithoura* var. *chiapasensis* bear an amazing resemblance to deeply lobed forms of *P. gilbertiana* or narrow-angled *P. apetala* Killip from Costa Rica, while others, especially the strongly variegated ones, closely resemble *P. boenderi* J. MacDougal. All these related southern Mesoamerican species have different flowers.

The flowers, light green with a mix of red, orange, and yellow, appear to be similar to the typical variety in coloration, but they are slightly larger. Although *Passiflora ornithoura* var. *ornithoura* always has two coronal rows, the inner row is sometimes reduced to only a few very small filaments. The new variety appears to have lost the inner row entirely in most populations; only in one specimen from Chimaltenango, Guatemala, was a second row seen, this reduced to only a few tiny members (*Johnston* 1107, EAP, but not the specimen at F). This variation in the expression of the inner coronal row is similar to that noted in the related *P. gilbertiana* (MacDougal, 1989).

The distribution and habitat of the two varieties show their adaptation to slightly different conditions. *Passiflora ornithoura* var. *chiapasensis* is a wet, cool montane entity, mostly from bosque mesófilo de montaña (moist montane forest) at 1800–2500 m from Chiapas, Mexico, and nearby Guatemala, with one record from Honduras. In Chiapas, Mexico, it is associated with *Magnolia*, *Quercus*, *Pinus*, *Matudaea*, *Billia*, *Styrax*, *Podocarpus*, *Turpinia*, and *Saurauia*. In contrast, the typical variety is commonly found in seasonally drier forest, even thickets in open grassy woodland, from 1200 to 1800 m, rarely to 2200 m. The geographic ranges of the two varieties are adjacent, with variety *ornithoura* apparently nested allopatrically within variety *chiapasensis*. At present, *P. ornithoura* var. *ornithoura* is known definitely only from central Guatemala and El Salvador, with one questionable record from Jinotega, Nicaragua (*P. Standley* 10970, F).

I am tempted to recognize this new entity as a species, especially given the marked ecological di-

vergence, but there is remarkably little well-preserved floral material among all the sheets of both varieties. The flowers, though apparently different in size and very similar in color, are actually poorly known due to the poorly prepared material.

The type locality and its flora were featured in an article by Matuda (1950), and the type specimen was cited there as *P. ornithoura* [as “*ornitheura*”]. The only other passionflower Matuda reported from the mountain was *P. rugosissima* Killip, growing about 200 m lower in elevation.

Phenology. Flowering and fruiting September to December, with fruiting continuing into February.

Etymology. The varietal epithet recognizes the state of Chiapas, Mexico, and the Sierra Madre de Chiapas mountain chain where the holotype was collected.

Paratypes. GUATEMALA. **Chimaltenango:** 8 mi. W of Patzicía on hwy. from Patzún, 14 July 1977, *T. Croat* 41080 (MO). **Escuintla:** Calderas, 24–25 Oct. 1937, *J. R. Johnston* 1107 (EAP, F); region of Los Positos, above Las Calderas, 16 Dec. 1940, *P. Standley* 80276 (F). **San Marcos:** en el camino Talquián–Cima del Volcán Tacaná por la vereda de los trigales, 19 Oct. 1985, *Martínez et al.* 14076 (MEXU, MO). MEXICO. **Chiapas:** SE side of Volcán Tacaná above Talquián, 12 Nov. 1972, *D. Breedlove* 29478 (DS); Siltepec, ridge above Siltepec on road to Huixtla, 18 Jan. 1973, *D. Breedlove & Smith* 31973 (DS, MO); 9.5 km SW of El Rosario along road to Ojo del Agua & Niquivil, 6 Nov. 1986, *D. Breedlove* 65626 (CAS); along S slopes of Sierra de Soconusco to crest, betw. Cañada Honda to El Triunfo, 6 Nov. 1945, *E. Hernández Xolocoti & A. J. Sharp* X-352 (DS, MEXU); Unión Juárez, en el camino Talquián–Cima del Volcán Tacaná, rumbo a la línea divisoria con Guatemala, 20 Oct. 1985, *Martínez et al.* 14159 (MEXU, MO); Siltepec, Jan. 1937, *E. Matuda* 928 (MEXU, MICH); Huixtla, Pizarrén, a 17 km al NW de Motozintla de Mendoza, camino a Siltepec, 20 Sep. 1983, *Téllez & Pankhurst* 6983 (MEXU, MO, WIS). HONDURAS. **Lempira:** Guamil, alrededor de El Súcte, 7 km al NE de San Manuel Colohete, en el Parque Nacional de Celaque, 16 Feb. 1993, *Mejía* 286 (BM, EAP, HEH, MO, TEFH).

Passiflora platyloba* Killip var. *pubescens (Grisebach) J. MacDougal, comb. nov. Basionym: *Passiflora serrulata* [var.] *β. pubescens* Grisebach, *Bonplandia* 6(1): 7, 15 Jan. 1858. TYPE: Panama. *Duchassaing s.n.* [1850–1851] (lectotype, designated here, GOET).

Passiflora platyloba var. *williamsii* (Killip) A. Gentry, *Ann. Missouri Bot. Gard.* 63: 342. 1976. Syn. nov. *Passiflora williamsii* Killip, *J. Wash. Acad. Sci.* 12: 262. 1922. TYPE: Panama. Coclé: Bismarck, above Penonomé, 600–925 m, 5–19 Mar. 1908, *R. S. Williams* 585 (holotype, NY, photo at B, US).

The species group of *Passiflora* centered around the well-known *P. maliformis* L. extends into lower

Mesoamerica from northern South America. Two Mesoamerican species were recognized by Killip (1938), *P. platyloba* Killip from Guatemala to Costa Rica, and the rare *P. williamsii* from Panama. Gentry (1976) concluded that separation at the species level was not warranted, and reduced *P. williamsii* to a variety of *P. platyloba*.

At the varietal rank the correct name is *Passiflora platyloba* var. *pubescens*. Grisebach (1858) described the taxon as variety *pubescens* of *Passiflora serrulata*, but Killip (1938), seizing upon certain inconsistencies in the protologue, put this name in synonymy with *P. vitifolia* HBK and erroneously designated for it a type at P that is the wrong species. The three-lobed leaves of the two are superficially similar. A close reading of Grisebach's protologue (1858: 7) shows it to perfectly and accurately describe the taxon we know as Killip's *P. williamsii*, but at the end there is the confusing note [translated from the Latin] “–the flowers, according to a colored painting by Duchassaing, appear to be the same shape and color as *P. vitifolia* Kunth.” *Passiflora vitifolia* has large bright red flowers, unlike any other passionflower in Central America. Without Grisebach's original material before him, Killip relied only on the protologue and gave more weight to the reference to the colored painting than to the rest of the protologue. Finding a Duchassaing specimen of *P. vitifolia* at P, Killip decided it was the type of Grisebach's *P. serrulata* var. *pubescens*.

The specimens in Grisebach's personal and original herbarium at GOET tell a different story, and require the selection of a lectotype from among the elements conserved there. There are three sheets of the taxon in question, all collected by Duchassaing in Panama. One has unlobed leaves (a known variation of the taxon), is labeled by Grisebach as “*P. serratifolia* L.,” and apparently is the basis for his inclusion of that name in his listing of *passifloras* from Panama (1858: 7). This sheet can be disregarded because neither the inscription nor the form of the leaves fits the protologue. On the remaining two sheets, both originally annotated with the same manuscript name, there are three elements. One sheet has leaves and immature fruits; the other sheet has leaves and floral bracts and buds, and a watercolor painting by Duchassaing pasted to the bottom of the sheet. That painting is of the leaf and scarlet flower of *P. vitifolia*. Grisebach undoubtedly used elements from both sheets to construct his varietal diagnosis, since fruits as well as floral material are mentioned. Only one sheet is marked with the new name, that with the color painting. Besides phrases identical to the pro-

tologue, there is also written there “[*Passiflora*] *serrulata* Jacq. var. *pubescens* m.,” all in Grisebach’s hand. I have therefore chosen this sheet, with the exclusion of the colored painting, to be the lectotype of *Passiflora serrulata* var. *pubescens*.

Passiflora quetzal J. MacDougal, sp. nov. TYPE: Guatemala. San Marcos: wet mountain forest near Aldea Fraternidad [ca. 14°56’N, 91°52’W], betw. San Rafael Pie de la Cuesta & Palo Gordo, W-facing slope of the Sierra Madre Mountains, 1800–2400 m, 10–18 Dec. 1963 (fl), L. O. Williams, A. Molina R. & T. P. Williams 25994 (holotype, EAP; isotype, ENCB, photo at DUKE, MEXU, MO). Figure 3.

Haec species characteribus foliaribus *Passiflorae membranaceae* incolis mexicanis similis, sed ab eis bracteis viridulis multo minoribus atque floris androgynophoro brevi distinguitur.

Vine, glabrous throughout; Stems terete, glaucous; prophylls of the vegetative bud 2, unequal, 1–3 × 0.6–1.5 mm, both narrowly ovate, long-acuminate, 3- to 5-toothed or entire. Stipules 10–19 × 10–20 mm, depressed ovate, auriculate, clasping, widely obtuse, abruptly acute and apiculate-mucronulate to abruptly long-acuminate, the margin entire to obscurely crenulate and 8–15-glandular; petioles (1-)2-glandular near or slightly proximal to the middle, the nectaries 0.6–0.8 × 0.4–0.9 mm, narrowed at base or not; blades 7–11.5 × 7.5–11.5 cm, subpeltate 2–3(–3.5) mm from the margin, entire, or glandular-denticulate at very base, not variegated at maturity, very widely obovate to widely elliptic or ± circular, at base extremely shallowly cordate to truncate or slightly rounded, shallowly to obscurely 3-lobed, angle between the lateral veins 40°–55°, the lateral lobes broadly obtuse to rounded or nearly obsolete, the central lobe obtuse or somewhat rounded to truncate; laminar nectaries marginal, 4 or 5 glands borne basally, (0)1 to 8 glands borne just proximal to the lateral veins, and (0)2 to 8 glands borne marginally distal to the lateral veins. Peduncles (1)2 per node, 3.6–5.8 cm, uniflorous; bracts 2 at apex of peduncle, 0.9–1.3 × 1.0–1.3 cm, ovate to widely ovate-oblong, cordate, free to the base, entire, 6- to 12-glandular marginally, obtuse to rounded, apiculate or abruptly long-acuminate, light green. Flowers white to green-white, the coronal color unknown; stipe 2.5–4 mm (to 5 mm in fruit); hypanthium diameter ca. 15 mm; sepals 18–20 × 9–10 mm, oblong triangular, rounded at apex, with no projection; petals 12 × 7 mm, ovate and notably narrowed at base; coronal

filaments in 2 to 3 series, the outermost 16–20 mm, filiform, the inner 1 to 2 series 7–10 mm (1 inner series at petals, 2 inner series at sepals); operculum 4.5–5.0 mm, membranous, plicate; limen edge at least 1.5 mm high; androgynophore 8.5–9 mm, the free staminal filaments ca. 6 mm, the anthers ca. 5 mm long; ovary 3.8–4.0 × 2.3–2.5 mm, ovoid-ellipsoid, glabrous; styles at least 9 mm long including stigmas. Fruit ca. 6 × 3.5 cm, ellipsoid, stipe absent or less than 4 mm; seeds 5.3–6.0 × 3.5–3.9 × 2.0 mm, obovate in outline, campylotropous, the testa reticulate with ca. 50 to 60 pits, the chalazal beak inclined toward the raphe.

Passiflora quetzal is assigned to supersection *Hahniopathanthus* in subgenus *Decaloba*, where it exhibits a number of character states primitive for that supersection. This new species vegetatively closely resembles certain forms of *P. membranacea* from Chiapas, Mexico, with subpeltate leaves, a pair of small stalked petiolar nectaries, and abundant marginal laminar nectary glands borne not just at the base of the lamina, but also marginally between the primary veins. These characteristics are primitive in the group, by outgroup comparison. Killip (1938: 23) did not observe glands in this group, stating “in these . . . species there are no nectar-secreting glands in any form” In reality, extrafloral nectaries are common in this group. The species are polymorphic for the presence and locations of various types of nectaries, and this variation gives valuable evidence about the relationships within each species and within the supersection. In the description above, the leaves lacking the marginal nectaries in some positions were smaller ones; the large leaves on all the specimens bear abundant glands. The flowers are similar to those of *P. guatemalensis* and to forms of *P. hahnii*, but the bracts are smaller. *Passiflora quetzal* does have only two floral bracts, an advanced state in the supersection and in subgenus *Decaloba*. The floral buds are obtusely and shallowly conical, like *P. guatemalensis*. I originally annotated the isotype (ENCB) as “aff. *cookii* Killip,” a name now considered a synonym of *P. hahnii* (see discussion above under *P. hahnii*). Several searches at the F herbarium for an expected isotype have been fruitless.

Distribution and habitat. Southwestern Chiapas, Mexico, and adjacent western San Marcos, Guatemala, on western slopes of the Serranía Transístmica, or Cordillera Madre, at 1800–2400 m in wet mountain forest or “bosque mesófilo de montaña” (moist montane forest). The type locality is also the type locality for *Passiflora eglandulosa* J. MacDougal.



Figure 3. Photo graph of the isotype of *Passiflora quetzal* at ENCB.

Etymology. This species is named for that splendor of the forest, the quetzal, and the native trogons that daily perch among the vines at the type locality. Following ICBN Article 23.2 (Greuter et al., 2000), I choose the epithet from the undeclined American English and Central American Spanish word for *Pharomachrus mocino*, the resplendant quetzal, taken from the Nahuatl word *quetzalli*.

Paratypes. MEXICO. **Chiapas:** Unión Juárez, en el

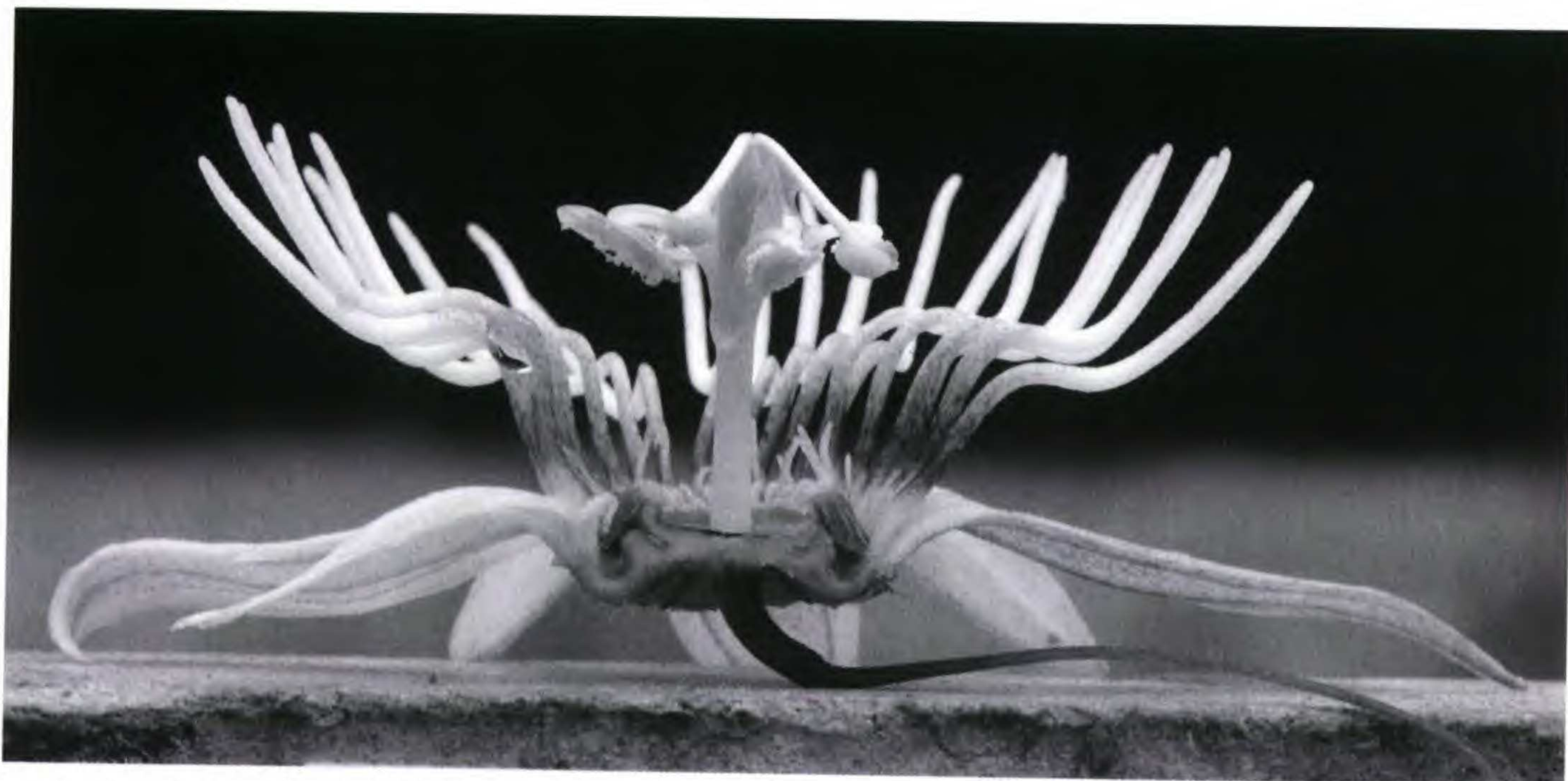


Figure 4. Photograph of a fresh flower of *Passiflora quinquangularis* in longitudinal section showing details of corona and curved floral stipe (MacDougal 626, DUKE).

Volcán Tacaná por el camino de Talquían a la cima del volcán, por la línea divisoria de Guatemala, 6 Feb. 1987 (bud, fr), *Martínez S. et al.* 19613 (MEXU), 19678 (MEXU, MO).

Passiflora quinquangularis S. Calderón ex J. MacDougal, sp. nov. TYPE: El Salvador. San Salvador: S of San Salvador, July 1922 (fl), S. Calderón 851 (holotype, US 1151809, photo at MO neg. 05129; isotypes, GH not seen, US). Figure 4.

Haec species *P. rubrae* et *P. capsulari* similis, sed ab eis caule quinquangulati atque alabastris modo araneae ex pedunculis pergracilis (minus quam 0.5 mm in diam.) pendentibus distinguitur.

Vine 2–4 m, herbaceous, or slightly woody at base, pubescent throughout, often densely so at shoot tip, on stem, and abaxial surface of leaves, sometimes the stems glabrescent with age; stems 5-angular, \pm cernuous at growing tip, pubescent with trichomes 0.3(0.4–0.6)–0.8 mm long; prophyll of the vegetative bud 1, linear-triangular to very narrowly lanceolate, 2.5–4(–7) mm long. Stipules 4–7 \times 0.4–0.9 mm, linear-triangular, falcate; petioles eglandular; blades 4–10(–17) \times 4–9(–12) cm, entire, not variegated, widely oblong-obovate (to widely oblong), 2(3)-lobed, the base slightly to strongly cordate, the lateral lobes acute to rounded, the angles between the lateral lobes (30°–)35°–45°(–60°), the central lobe (obtuse) rounded to truncate to obsolete; laminar nectaries absent. Inflorescences sometimes present in older plants as nearly leafless condensed lateral branches; peduncles 1 (very rarely 2) per node, (1.5–)3–5.5(–9.3) cm, very slender,

less than 0.5 mm diam., uniflorous, not bracteate; buds abruptly acuminate or short-beaked. Flowers green-white or cream, with a light purple center, the corona white with purple, with fruity sweet odor reminiscent of raspberries; stipe 3–5 mm (to 7 mm in fruit); hypanthium 8–10.5 mm diam.; sepals 15–21(–29) \times 5.4–7.0 mm, narrowly triangular, long-acuminate but with no projection, pale green-yellow to yellow-green, abaxially sparsely pilosulous especially on the 3 conspicuous nerves, light yellow-green and often flushed with minute red spots; petals 10–15 \times 3.0–4.3 mm, lanceolate, acuminate (or rounded at very apex), white or pale green-yellow; coronal filaments in 2 series, the outer 11–18 mm, filiform, slightly attenuated and white in distal half, light red-purple to purple-red proximally, purple-red basally, the inner 3–4.5 mm, capillary, red-purple, clavate at the paler tip; operculum ca. 2 mm high, membranous, plicate, light purple to medium red-purple, white apically; limen floor very pale red-purple; nectar ring (annulus) present in nectary chamber, ca. 1 mm high, dull purple, not bright yellow; androgynophore (7–)8–10 mm, strictly uncolored except for trace of chlorophyll, the free staminal filaments 4.5–5.5 mm, not colored, anthers 3.7–4.2 mm long, not colored; ovary 2.3–4.0 \times 1.7–2.3 mm, ellipsoid, slightly 6-ridged, minutely densely puberulent; styles 5–6.5 mm long including stigmas. Fruit 3–4.5(–6) \times 1.5–2(–3) cm, including a ca. 3 mm stipe, broadly fusiform to ellipsoid, conical at both ends or apically with a beak, acutely 6-carinate with keels ca. 1–2 mm high, yellow-green, slightly short-puberulent with trichomes

0.1 mm or less, dehiscent; seeds $3.4\text{--}4.0 \times 1.7\text{--}2.4$ mm, transversely sulcate with 6 or 7 (or 8) sulci, the intervening ridges not rugulose.

This species is notable for its long (to 5.5 cm or longer) and diagnostically very slender peduncles (less than 0.5 diam.), upon which the acuminate or short-beaked buds and the flowers are pendent. Due to the curvature of the floral stipe (cf. Fig. 4), however, the flowers face horizontally to open. In *Passiflora*, it belongs to section *Xerogona* (Rafinesque) Killip in subgenus *Decaloba* based on the plicate operculum, absence of laminar nectaries or floral bracts, the carinate apically dehiscent fruit, and the seeds' smooth transverse ridges. Most similar to forms of *P. rubra* L., *P. quinquangularis* differs significantly by its slender floral peduncle and resulting floral orientation, the 5-angled stem, and the only minutely puberulent, not conspicuously pubescent, ovary. Although *P. rubra* does not occur in Mexico or Central America, another close relative does, *P. capsularis* L. This species prefers wetter habitats than *P. quinquangularis*, but in a few places in Guatemala they grow within a km of each other (pers. obs.). *Passiflora capsularis* is easily distinguished from the new species by its pure white or cream, unmarked flower that is borne upward on a stout peduncle, less pubescence overall, and the 3- to 4-angled stem.

As in many species of *Passiflora* subg. *Decaloba*, the vestiture is composed of two different classes of trichomes: very short, curved, cylindrical to clavate antrorsely appressed trichomes 0.08–0.12 mm long (Harms, 1893; MacDougal, 1994), and longer, straighter, pointed ones, in this case 0.3–0.8 mm long. The ovary, for example, has only the short curved type, while most other surfaces of the plant have a mix of the two.

Specimens of this new species have been cited by a number of authors under the name *Passiflora capsularis*, and the descriptions of that species in florulas of Central America, as well as in Killip's (1938) monograph, have included measurements and character states from the new species. The illustration of *P. capsularis* in Standley and Williams (1961), except for the separate fruit, is actually wholly of this species.

A cleared leaf of *Passiflora quinquangularis* from *J. MacDougal* 626 (MO) was studied and illustrated by Klucking (1992: 243–244, pl. 96, fig. 3), under the abbreviated names, "P. quing." and "P. quing- -" [sic]. Katie Hansen (pers. comm.) reports that the chloroplast intron rpoC1 is lacking in samples of *J. MacDougal* 626 (MO). This clone, imported live from Guatemala in 1980, was grown and widely

distributed. It was self-incompatible in the greenhouse. It appears to be the only clone in cultivation even now, and has been listed in many nursery catalogs and illustrated in color in a few popular books (e.g., Ulmer & MacDougal, 2004; Vanderplank, 1996, 2000).

Named for its 5-angled stem, *Passiflora quinquangularis* has its origin in a short obscure publication by Salvador Calderón, a publication that survives by only a single known partial copy. It would have been lost to science except that it was seen and cited by the monographer Killip (1936, 1938) while he worked at the US herbarium. Killip cited both text and figures when, as a synonym of *P. capsularis*, he invalidly published "*Passiflora quinquangularis* Calderón, *Passifloras Dilobatas del Salvador* 6." A more complete citation would be, *Datos Bot. Médica El Salvador (Passifloras Dilobatas de El Salvador)* 6, figures 1–8.

Salvador Calderón (1884–1940), a Salvadorian botanist and chief of Agricultural Botany of his country, collected plants in collaboration with Paul C. Standley of the Field Museum for a flora of El Salvador. He was the Salvadorian contact for botanists from the United States in the 1920s and early 1930s, and published articles and booklets between 1925 and 1929 on botany, agriculture, and geology. The seven-page protologue of his *P. quinquangularis* is one of the more detailed ever published for a passiflora, with astute observations on anatomy, phyllotaxy, plant movement, ptyxis, floral morphology, chirality, seed morphology, and more.

The publication that heralded this passionflower was never widely distributed and appears to be generally lost. After much correspondence, I can locate only one partial copy in the reprint collection of the United States National Herbarium at US. It is a booklet with the title *Datos Para La Botánica Médica de El Salvador* and the author's name on the cover. Also on the cover is "Escuela de Medicina, Química y Farmacia/San Salvador, República de El Salvador, América Central." Inside, the work is entitled *Passifloras Dilobatas de El Salvador* and runs from page [1–4 missing] 5 to 20, where the article clearly continues but is not present in this bound copy. There are line drawings and two tipped-in color plates. There is no date. It might have been published during his productive period in the 1920s, an idea also supported by the fact that herbarium specimens (F, US) of all taxa collected by Calderón are dated between 1921 and 1929, with a very few from 1931. Killip cited the publication in both 1936 and 1938; allowing for time in manuscript, Killip may well have seen it before 1935. This date is critical because *P. quin-*

quangularis was published in Spanish, without the Latin diagnosis required after 1934 for valid publication. It probably beats this cutoff date, but it hardly matters, for there is little question that due to the extreme rarity of the publication, the name is not effectively published (Greuter et al., 2000, ICBN Art. 29.1).

The decision that *Passifloras Dilobatas de El Salvador* was not effectively published and distributed invalidates two infrageneric botanical names that were otherwise newly and probably validly published there: "*Passiflora* subsection *Pubescens*" S. Calderón and "*Passiflora* subsection *Raripilus*" S. Calderón. Two other species names are invalidated: the already doubtfully valid "*Passiflora subtriangularis* (no rank) *beta*" S. Calderón [= *P. bicornis*], and the definitely invalid "*Passiflora subtriangularis* (no rank) *alfa*" S. Calderón. This last was published with *P. salvadorensis* J. D. Smith [= *P. jorullensis* var. *salvadorensis*] in synonymy. Calderón made no reference to any of these new botanical names in his two other more widely known botanical publications (Standley & Calderón, 1925, 1941), probably because Killip was a collaborator for the passionflowers there.

Regarding *Passiflora quinquangularis*, Calderón did not cite any specific specimens in his booklet, except to say that his description was based on wild plants found in the highlands around the capital (San Salvador). Only two preserved collections of this species by Calderón are known, and only one, *Calderón 851* (GH, US [2]), is from the area of San Salvador. Killip (1936), treating *Passiflora quinquangularis* as a synonym of *P. capsularis*, rightfully chose this collection as the "type," and in 1938 noted that these specimens were held at GH and US. At one time I thought the name to be valid and effective, and thus in 1989 had annotated one sheet at US as lectotype; to avoid future confusion, I now designate the same sheet to be the holotype.

Distribution and habitat. *Passiflora quinquangularis* is found in seasonally dry forest, brushy hillsides, hedges and secondary vegetation, oak with pine forest, and "ecotone de selva baja caducifolia y bosque mesófilo" (ecotone of low deciduous forest and moist forest) at elevations of 580–1600 m sporadically from Oaxaca, Mexico, to El Salvador, with a disjunct population known from the Nicoya Peninsula of Costa Rica. It is not recorded from Honduras or Nicaragua. Only in El Salvador and southwestern Guatemala does it seem to be common.

Phenology. Flowering and fruiting throughout the year.

Common names. *Ala de murciélago* (R. Villa-

corta et al. RV854), *bejuco calzoncillo* (J. González 331), *calzoncillo* (Calderón 851), *bejuco calzón de mujer* (F. Chinchilla s.n.), *bejuco calzón de hembra* (J. González 409). These all refer to the curious shape of the bilobed leaf.

Paratypes. COSTA RICA. **Guanacaste:** La Cruz, Santa Elena, Parque Nacional Guanacaste, 2001, A. Estrada s.n. (CR, MO photo). EL SALVADOR. **Ahuachapán:** 1928, S. Calderón 2428 (F); San Benito, al N del Escobal, Parque Nacional El Imposible, 13°49'N, 89°56'W, 27 Apr. 1994, F. Chinchilla s.n. (B, LAGU, MO), R. Villacorta et al. RV854 (LAGU, MO); near Ataco, 19 Jan. 1947, P. Standley & Padilla 2644 (F); vicinity of Ahuachapán, 9–27 Jan. 1922, P. Standley 19733 (MO, NY, US). **La Libertad:** Teotepque, 13°25'N, 89°31'W, 4 May 1996, J. González 331 (MO); Jayaque, 13°40'N, 89°26'W, J. González 409 (B, EAP, LAGU, MO, UES); Finca El Paraíso, Jayage, 13 July 1976, Montalvo 4711 (MO). GUATEMALA. **Baja Verapaz:** Salama Puente Barranca, al W de Salama, 15°06'N, 90°18'W, 24 July 1988, P. Tenorio et al. 14740 (MO). **Santa Rosa:** Cuajiniquilapa, Sep. 1893, Heyde & Lux s.n./J. D. Smith 6142 (US); cultivated at Duke University 1980–1984, from live stems collected 27 Jan. 1980, 6 mi. E of rd. to Cuilapa on CA-1, ca. 3 mi. W of intersection of CA-1 with CA-8 to Valle Nuevo, pressed July 1983, J. MacDougal 626 (BH, BM, COL, CR, DUKE, F, G, GOET, MEXU, MO, MO-spirit, UPCB, US, UVAL); along road SE of Barberena, 21 Nov. 1940, P. Standley 77729 (F, US); near Cuilapilla, 23 Nov. 1940, P. Standley 78118 (F). MEXICO. **Oaxaca:** Lachigüiri, cerca a Santiago Lachigüiri, 9 June 1985, M. Chazaro & M. Leach 3371 (WIS); Juchitan, 1 km al S de Guevea de Humboldt, 16 Mar. 1983, R. Torres et al. 2521 (MEXU).

Passiflora sexflora Jussieu, Ann. Mus. Natl. Hist. Nat. 6: 110, pl. 37, fig. 1. 1805. *Decaloba sexflora* (Jussieu) M. Roemer, Fam. Nat. Syn. Monogr. 2: 164. 1846. TYPE: Dominican Republic. Santo Domingo, Poiteau s.n. (holotype, P).

Passiflora obscura Lindley, Trans. Roy. Hort. Soc. London 7: 48. 1830. Syn. nov. *Decaloba obscura* (Lindley) M. Roemer, Fam. Nat. Syn. Monogr. 2: 157. 1846. TYPE: Cultivated in England from seeds brought from "some part of the North Eastern Coast of South America" by G. Don in 1823, *Herb. J. Lindley* (holotype, CGE, photo at MO neg. 05119).

Examination of type material of *Passiflora obscura* shows this name to be a synonym of the earlier *P. sexflora*. Killip (1938), not having seen this type, aligned the name doubtfully under *P. rubra*. These two species are often vegetatively very similar, with pubescent more or less bilobed leaves with no laminar nectaries, but are unmistakable with fertile material. *Passiflora sexflora* has bracts on the usually branched peduncles, and purple berries, while *P. rubra* has naked, non-bracteate, unbranched peduncles, and a red, pink, or white and red dehiscent berry-like capsule.



Figure 5. Photograph of the holotype of *Passiflora subfertilis* at F.

Passiflora subfertilis J. MacDougal, sp. nov.
TYPE: Guatemala. Quezaltenango: betw. Finca Pirineos & Finca Soledad, along stream, lower S-facing slopes of Volcán Santa María, betw. Santa María de Jesús & Calahuaché, 1300–

1400 m, 5 Jan. 1940 (fl, imm. fr), J. A. Steyermark 33503 (holotype, F). Figures 5, 6.

Haec species *Passiflorae biflorae* similis, sed ab ea gemma vegetativa prophyllum unicum gerente, folii lobis



Figure 6. Flowers of *Passiflora biflora* compared to the flower of *P. subfertilis*. From left to right, flowers from three clones of *P. biflora* (Costa Rica, *MacDougal* 463 (DUKE); Costa Rica, *MacDougal* 464 (DUKE); Guatemala, *MacDougal* 598GR (DUKE)), and flower of *P. subfertilis* (*MacDougal* 597GR). Scale is in cm.

acuminatis acutisve atque petalis sepalisque angustioribus distinguitur.

Vine 2–4 m, minutely puberulent throughout at the shoot tip, or the blades sparsely so, sparsely puberulent to glabrescent below; stem subterete or slightly angular, striate; prophyll of the vegetative bud 1, 1.2–2.0 mm long, narrowly lanceolate, entire, sometimes curved over the bud. Stipules $1.6\text{--}2.1 \times 0.2\text{--}0.3$ mm, linear-triangular, falcate, stramineous-necrescent; petioles eglandular; blades $2.8\text{--}6 \times 5\text{--}9.5$ cm, in outline obovate to widely obovate, shallowly 2-lobed (rarely sub 3-lobed), the base subtruncate to obscurely widely cordate, the lateral lobes acuminate to acute, the central lobe absent or when present obsolete to obtuse, the angle between the lateral veins $50^\circ\text{--}72^\circ$, the ratio of laminar width to central vein length 1.1–2.1, not variegated, the margin entire; laminar nectaries numerous but inconspicuous, borne between the main veins; juvenile leaves in outline deeply depressed obovate, deeply 2-lobed, the base broadly rounded to subtruncate, the lobes very widely spreading, lanceolate to narrowly triangular, acuminate, the angle between the lateral veins $70^\circ\text{--}115^\circ$. Peduncles (1)2 per node, 0.8–1.0 cm, uniflorous; bracts $0.8\text{--}2.0 \times 0.1\text{--}0.2$ mm, linear-triangular, early stramineous-necrescent; buds slightly constricted just distal to hypanthium. Flowers white, the corona light yellow; stipe 5–7 mm (to 9 mm in fruit); sepals $13\text{--}15 \times 6\text{--}7$ mm, ovate-oblong, pale green abaxially, \pm white adaxially, with no projection; petals $10\text{--}12 \times 4$ mm, narrowly oblong, white; coronal filaments in 2 series, the outer 5–6 mm long, slightly laterally compressed, basally yellow-green, distally light yellow, the inner ca. 2.5 mm, capillary, capitellate, near-white with white to green tips; operculum membranous, plicate; androgynophore ca. 9 mm, slightly purple; ovary glabrous, styles and stigmas green. Mature fruit unknown; immature

fruit $2\text{--}2.5 \times 1.5\text{--}1.8$ cm, widely ellipsoid to widely obovoid, not stipitate; arils unknown; seeds apparently transversely sulcate.

This rare species was known only from two collections made at one place by Steyermark until I went to, or close to, that locality in 1980 and collected it alive. I was then able to cultivate, study, and photograph the species in the greenhouse. Assigned to section *Decaloba* of subgenus *Decaloba*, it is generally very similar to the sympatric *Passiflora biflora* Lamarck. The historic monographer Killip had annotated the two older collections as *P. biflora*, but it may be distinguished easily from that species by having only one prophyll at the vegetative bud and leaves with sharply pointed lateral lobes. The flowers are very similar, but the buds of *P. subfertilis* are constricted distal to the hypanthium, unlike the buds of *P. biflora*. In Figure 6, three clones of *P. biflora* from Guatemala and Costa Rica showing a range of floral variability in that species are compared to a flower of *P. subfertilis*. The flower adjacent to that of *P. subfertilis* is from a *P. biflora* collected at the exact same locality. The petals of the new species are proportionally narrower than those of *P. biflora*. The foliage very much resembles that of the rare *P. sanctae-mariae* J. MacDougal, described from a locality only 1 km distant, except *P. subfertilis* has numerous inconspicuous laminar nectaries. These nectaries can be seen in the cleared leaf from *MacDougal* 597GR (MO) that was studied and illustrated by Klucking (1992: 253–254, pl. 109, fig. 4), as “*Passiflora subfertilis* [MacDougal].” It also vegetatively resembles *P. helleri* Peyritsch, with which it grows, and the prophyll of the vegetative bud is often curved over in the same way. This species has a floral corona of only one row; however, its leaves have a narrower angle of lobing, from $24^\circ\text{--}40^\circ$ ($\sim 50^\circ$), and the leaves are

nearly always longer than wide, with a width to length ratio of 0.55–0.85(–1.0). Because the new species resembles the three sympatric species mentioned and is only known from a very small area, I wondered if it might be a hybrid. Hybrids are rare in the genus, but are suspected in the *P. sexflora* Jussieu–*P. rugosissima* Killip complex in Veracruz and Oaxaca, Mexico, and in the widespread Neotropical *P. foetida* L. and *P. ciliata* Aiton complexes. Morphologically, it is not clearly intermediate between any of the three potential parents, though one of the parents would certainly be *P. biflora* (cf. Fig. 6). If it is a hybrid, it is either reproducing or is being regenerated around the type locality, for the plant I found was only a few years old, and probably not a vegetative sprout of the same plant Steyermark found 40 years earlier. In the greenhouse, fresh pollen showed only 40%–50% viability as indicated by lactophenol-cotton blue staining (slide preserved on sheet at MO). Based on this, I give the name *subfertilis*, and although there is some suspicion that it is a hybrid, it is not here published as one.

The type and paratype localities in Guatemala are no more than a kilometer from each other on the Pacific slopes of Volcán Santa María, in disturbed primary and secondary regrowth of premontane moist forest at 1250–1400 m. Associated there, besides the species discussed above, are the rare *Passiflora prolata* Masters, and within 1 km, *P. hahnii*. Local vernacular names recorded on Steyermark's labels are *murciélagos de montaña* and *granadilla*.

Paratypes. GUATEMALA. **Quezaltenango:** ca. 6 km below Santa María de Jesús on Rt. 9S, near km post 196, 19 Jan. 1980 (juv.), J. MacDougal & Miley 597 (DUKE, F, MEXU, MO, UVAL), [thereafter cultivated at Duke University 1980–1983 as J. MacDougal 597GR (DUKE, MO)]; betw. Finca Pirineos & Finca Soledad, along stream, lower S-facing slopes of Volcán Santa María, between Santa María de Jesús & Calahuaché, 5 Jan. 1940 (fl), J. A. Steyermark 33591 (F).

***Passiflora sub lanceolata* (Killip) J. MacDougal, comb. et stat. nov.** Basionym: *Passiflora palmeri* var. *sub lanceolata* Killip, Publ. Carnegie Inst. Wash. 461: 322. 1936. TYPE: Guatemala. Petén: Uaxactún to San Clemente, 30 Apr. 1931, H. H. Bartlett 12788 (holotype, US 1492638; isotype, MICH).

This species has vividly colored flowers variously described as intense rose, bright purple-pink, or hot pink. The androgynophore is long (17–21 mm) and the white or white with pink or purple corona is reduced to 10 mm long or less. It is humming-

bird-pollinated, as was documented by Janzen (1968, as undetermined *Passiflora* sp.). From the three specimens known to him, Killip named this as a variety of *Passiflora palmeri* Rose, a white and violet-flowered subshrub endemic to Baja California. We now have abundant material, as well as a better understanding of the habitat differences between the desert in Baja California and the wetter though seasonally dry Yucatán Peninsula, that shows these to be distinct. *Passiflora sub lanceolata* is now known from Tabasco, Mexico, to northeastern Belize, and is in cultivation.

***Passiflora veraguasensis* J. MacDougal, sp. nov.** TYPE: Panama. Veraguas: along road betw. Escuela Agrícola & Alto Piedra (above Santa Fe) & Río Dos Bocas, ca. 5–8 km from Escuela, 730–770 m, 26 July 1974 (bud, fl, imm fr), T. B. Croat 25908 (holotype, MO 2292671). Figure 7.

Haec species *Passiflorae nelsonii* similis, sed ab ea foliis bracteisque minoribus, nectariis petiolaribus paucioribus minoribusque atque seriebus coronalibus duabus extimis inter se longitudine accedentibus distinguitur.

Vine, glabrous throughout except the bracts, sepals, and styles; stems terete; prophyll of the vegetative bud 1, widely triangular, obscurely glandular-dentate. Stipules 11–17 × 3.5–6 mm, oblong-lanceolate to oblong-ob lanceolate, acuminate to acute, deciduous, both margins glandular-serrulate; petioles not glandular or 1- to 3(to 4)-glandular near or just below the apex, the nectaries 0.8–1.2 × 0.8–1.7 mm; blades 8.5–13 × 6.5–11 cm, entire to obscurely glandular-denticulate especially near the base, not variegated, sometimes glaucous abaxially, (ovate to) widely ovate, unlobed, abruptly acuminate; laminar nectaries marginal, obsolescent except at the laminar base. Peduncle 1 per node, 2.1–4.5 cm, uniflorous; bracts 4.7–5.6 × 2.8–3.2 cm, connate 1.0–1.6 cm at the base, ovate, acute to abruptly short-acuminate, glabrous except for a narrow band of tomentum along the adaxial margin, the margin minutely glandular-serrulate to subentire. Flowers green-white, the corona purple (“dark lavender,” T. Croat 25908); stipe 10–13 mm, deeply recessed into the hypanthium base; sepals 25–28 mm, the margins and apex sparsely pubescent, the subapical projection 1.5–2.0 mm long; petals ± equal to sepals in length, green-white; coronal filaments in 10 to 11 series, the outermost 17–21 mm, the next 11–13 mm and thicker than the outermost, the inner 8 to 9 series 0.7–3 mm long; operculum 4.7–5 mm long, basally connate and membranous, filamentous in distal 2/3; andro-

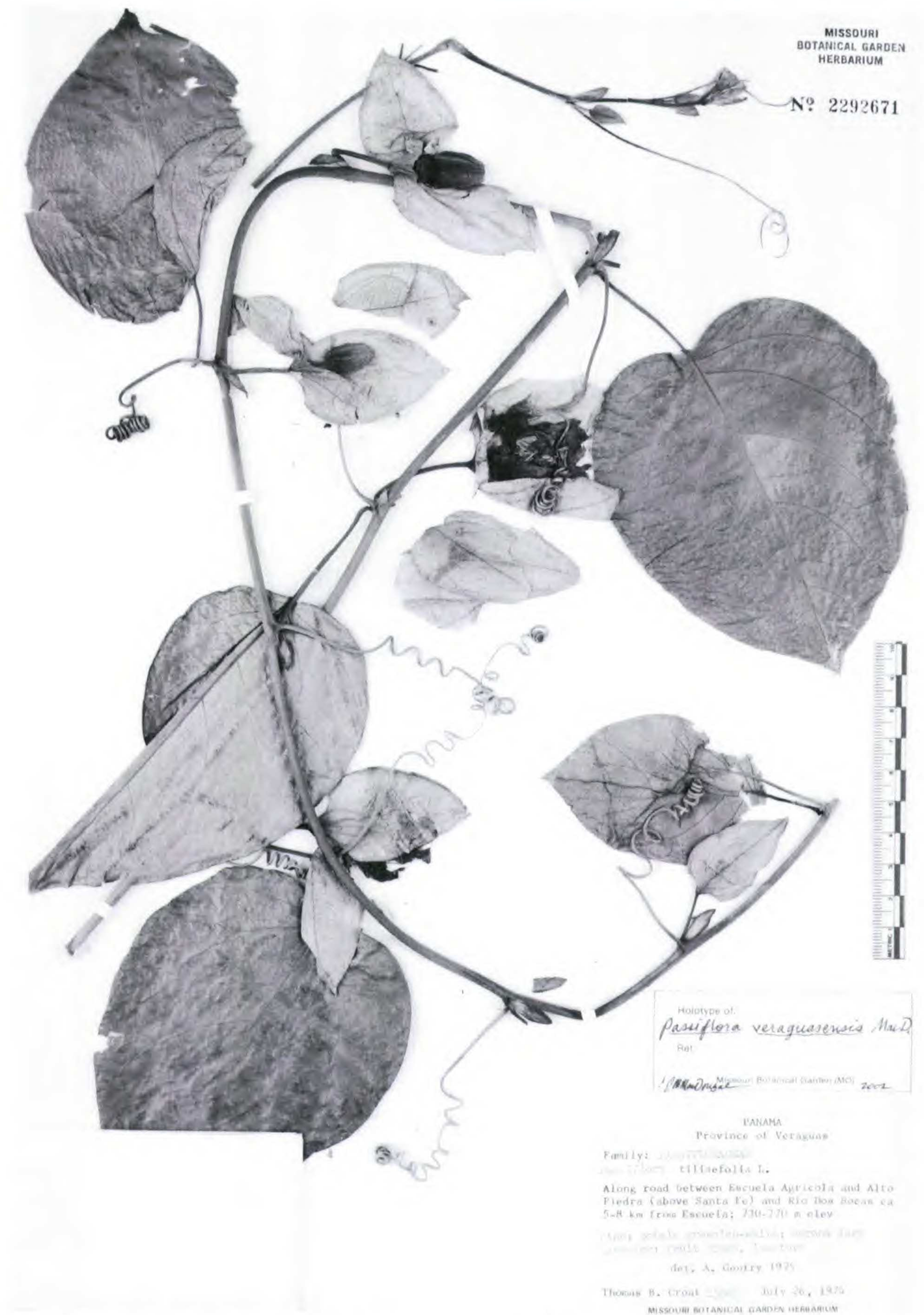


Figure 7. Photograph of the holotype of *Passiflora veraguasensis* at MO.

gynophore 8.5–9 mm, anthers 8–9 mm long; ovary 4.5–5 × 3–4 mm, ellipsoid, glabrous; styles short pubescent adaxially. Fruit ca. 6 × 5 cm, widely ellipsoid, exocarp thin, color unknown, not stipitate; arils unknown; seeds 10.0–10.5 × 6.0–7.0 mm, shallowly alveolate with 18 to 25 pits, sur-

rounded by 1–2 mm wide almost winged, flattened margins that are striate-dentate, the prominent chalazal beak antiraphal, the micropylar end notched or retuse.

Passiflora veraguasensis is most like the more

northern *P. nelsonii* Masters & Rose, and like it, is assigned to subgenus *Passiflora*, supersection *Laurifolia* (Cervi) Feuillet & J. MacDougal, series *Tiliafoliae* Feuillet & J. MacDougal. *Passiflora nelsonii* ranges from Veracruz, Mexico, to northeastern Costa Rica. *Passiflora veraguasensis* is apparently restricted to Panama. It is generally smaller vegetatively, and differences include the smaller bracts ($4.7\text{--}5.6 \times 2.8\text{--}3.2$ cm vs. $5.0\text{--}7.5 \times 3.0\text{--}5.0$ cm) and petiolar nectaries reduced in number and size (none or 1 to 3, rarely 4 glands vs. 4 or 5, rarely 6 glands that are 1–1.5 mm wide vs. 2–4 mm wide). In the new species, the two outer series of coronal filaments are more similar in length, with the outer twice or less as long (outermost 17–21 mm, the next 11–13 mm). *Passiflora nelsonii* has its outermost coronal row 3 to 10 times longer than the next row (outermost 18–22, the next 1–7 mm).

This new species was discussed by Gentry (1976) under the name *Passiflora tiliaefolia* L., and the present type collection was cited as a range extension of that species from South America. Gentry said the operculum appeared to be entire, but it is actually filamentous for more than half its length. Gentry's misapplied name was repeated in D'Arcy (1987). The butterfly *Heliconius cydno* (Nymphalidae) is recorded on the label of Knapp 5765 (MO) as an herbivore.

Distribution and habitat. *Passiflora veraguasensis* is found in western Panama near the Continental Divide at 730–1000 m in premontane moist to pluvial forest, at forest edges, and in forest gaps.

Phenology. Flowering April through September, fruiting June through December.

Etymology. The species is named for the Panamanian province of Veraguas, where it was first collected.

Paratypes. PANAMA. **Chiriquí:** al E del sitio de presa en Fortuna, 6 May 1976, Mendoza 312 (MO). **Coclé:** hills N of El Valle, E slope & ridges leading to Cerro Gaital, 27 June 1982, S. Knapp 5765 (MO). **Veraguas:** 2/10 mi. beyond fork in road at Escuela Agrícola Alto Piedra on road to Río Calovebora, 3 Apr. 1976, T. Croat & J. Folsom 33857 (MO); forest & forest remnants to 12 km NW of Santa Fé de Veraguas, 6 Dec. 1975, W. D'Arcy 10346 (MO).

Acknowledgments. Much of this work was started while a postdoctoral researcher for the *Flora Mesoamericana* project at the Missouri Botanical Garden with support from the Jessie Smith Noyes Foundation. I thank the curators of BH, BM, C, CAS, CR, DUKE, DS, EAP, ENCB, F, GH, GOET, K, LAGU, LL, MEXU, MICH, NY, TEFH, US, and WIS for permitting the long-term loans necessary for this study. Roy Gereau most generously trans-

lated the diagnoses of the new taxa into Latin, and Fred Keusenkothen of the MO web group scanned the illustrated herbarium specimens. George Pilz provided invaluable measurements from the EAP herbarium. Our understanding of some of the species here was greatly enabled through their cultivation, and I am indebted to the staff of the Duke University greenhouses many years ago for their assistance in caring for those living collections. Donald E. Stone and Melvin D. Turner provided critical support and analysis for this study. Ruth F. Schalbert, librarian at the Smithsonian Institution for many years, discovered the only known copy of Calderón's *passiflora* publication. I am also indebted to Peter M. Jørgensen, Gerrit Davidse, Jan Meerman, Connie Wolf, Kristen Porter-Utley, B. Hansen, and Katie Hansen for assistance. Charlotte Taylor and an anonymous reviewer improved the manuscript. Finally, I thank Robert Magill for unfailing support and access to the special research facilities at the Missouri Botanical Garden.

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